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Leles, Daniela; Reinhard, Karl; Fugassa, Martín Horacio; Ferreira, Luis Fernando; Iñiguez, Alena M.; and Araujo, Adauto, "A parasitological paradox: Why is ascarid infection so rare in the prehistoric Americas?" (2010). *Karl Reinhard Papers/Publications*. 20. <http://digitalcommons.unl.edu/natresreinhard/20>

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A parasitological paradox: Why is ascarid infection so rare in the prehistoric Americas?

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Abstract

Ascaris lumbricoides (giant roundworm) and *Trichuris trichiura* (whipworm) are the most common intestinal parasites found in humans worldwide today and they almost always co-occur. However, we find two distinct patterns in archaeological material. In historical North American and Old World contexts, the association of *A. lumbricoides* and *T. trichiura* is similar to the modern epidemiological picture. In contrast, the co-occurrence of *A. lumbricoides* and *T. trichiura* eggs in prehistoric South America is rare. For prehistoric contexts, *T. trichiura* is the most common parasite found in archaeological material. Recently molecular biology techniques pointed to a subdiagnosis of roundworm infection in pre-Columbian South American populations. This is contrary to the modern epidemiological picture in which *A. lumbricoides* infection is predominant. This is a paradox, especially when one considers the number of eggs laid by female daily, 200,000 and 20,000 thousand per day, for *A. lumbricoides* and *T. trichiura* respectively. By reviewing the records of these parasites, this paradox is presented and explanations for the paradox are explored. Taphonomy, prehistoric behavior patterns and medicinal plant use seem to be most relevant to the explanation of the paradox. Nematophagous fungi is a less likely factor creating the near absence of *A. lumbricoides* eggs in the prehistoric New World.

Keywords: Pathoecology, Paleoparasitology, Archaeoparasitology, Ascariasis, Trichuriasis, Coprolites, Parasitism, Taphonomy

Among human intestinal parasites, *Ascaris lumbricoides* (Linnaeus, 1758) is the most prevalent and has worldwide distribution (Crompton, 1999). *A. lumbricoides* has several common names including giant roundworm and maw-worm. It is most commonly associated with *Trichuris trichiura* (Linnaeus, 1771) which is known as whipworm (Chan et al., 1994; Saldiva et al., 1999). This association of *A. lumbricoides* and *T. trichiura* is due to similar transmission mechanisms and metabolism of the parasites, occupation of nearly the same niche outside human host, and high number of eggs laid per day. As reviewed by Gonçalves et al. (2003); Bouchet et al. (2003) both *A. lumbricoides* and *T. trichiura* are also the parasites most commonly found in archaeological material. However, for prehistoric America, this association is quite rare in contrast to historic archaeology in North America (Reinhard, 1990)

Paleoparasitology is the study of parasites found in archaeological or paleontological material (Ferreira et al., 1979). In a broad sense, paleoparasitologists study the evolution of parasite-host-environment relationships, as well as the origin and evolution of infectious diseases in a paleoepidemiological

perspective (Araújo et al., 2003). Archaeoparasitology (Reinhard, 1990) and pathoecology (Martinson et al., 2003; Reinhard, 2008; Reinhard and Bryant, 2008) address behavior and cultural influences of prehistoric people on parasite ecology. The theories of paleoparasitology and archaeoparasitology are relevant to the *Trichuris-Ascaris* paradox in prehistory

The low occurrence of *A. lumbricoides* and *T. trichiura* eggs in prehistoric American sites has long been noticed. Fouant et al. (1982), working with mummies from the Andes, noted the rarity of eggs of these species. She discussed the possibility that dry climate might be responsible for the low number of eggs found in Peruvian archaeological sites. In South America desiccation is the main mode of preservation. Dry conditions prevailed in the majority of South American archaeological sites

We performed a systematic bibliographic research for the finds of *A. lumbricoides* and *T. trichiura* in ancient material. Taphonomic, ecological, environmental, and diagnostic aspects of the papers are summarized and discussed below. Differences observed between ancient and present day distribution may be explained by these aspects

1. Materials and methods

Two reviews were used to conduct this research (Bouchet et al., 2003; Gonçalves et al., 2003). Electronic databases searched up to January 2009 were also used (PubMed, Isi Web of Science, Scopus, Ovid, Web Wilson, and Scielo). Manual search in index data base (Zoological Records, Tropical Diseases Bulletin, Biological Records), and consultations with specialists were also used. All references that fulfill inclusion criteria were evaluated. For electronic search the following words were used: "Ascaris", "Trichuris", "coprolite", "sediment", "soil", "latrine", "cesspit", "pit", "barrel", "privy", "remains", "archaeology", "archaeoparasitology", "paleoparasitology", "paleopathology", "excavation", "years ago", "before present", "history", "colonial", "pre-Columbian", "medieval", "middle age", "Iron age", "Bronze age", "Roman age", "Roman period", "ancient disease", "ancient parasites", "burial", "skeleton", and "mummy". Logical operators "AND" and "OR" were used to combine descriptors and track publications, as well as symbols "\$" and "*" to cut off key-words in order to search all derivations

Initially, 88 articles were included by the criteria used, but another screening was applied: (a) the finding of *A. lumbricoides* and/or *Trichuris* in ancient material of human origin; (b) the findings dated archaeologically to the 19th century or before, (c) no historical document was taken into account, (d) all types of publications were included, such as scientific meeting abstracts, letters and comments in scientific journals, (e) there were no limits for the year of publication and languages

The following data were observed and recorded from each article:

1) Geographical location of the finding, 2) archaeological date, 3) type of research material such as coprolite, sediment, or other kinds of remains, 4) quantification of eggs, 5) use of medicinal plants, 6) presence of fungi, 7) infertile eggs, 8) taphonomic descriptions, 9) environment and any other aspect concerning organic remains preservation

Sites that were negative for both of the study species were not included in the study

2. Results

Of 88 articles initially selected, 65 article abstracts were read, and after evaluation, 44 articles were fully studied. Next, all reviews and articles accessed by manual search were added, totaling 98 articles concerning this research

The findings of *A. lumbricoides* and *T. trichiura* eggs in ancient material of human origin are summarized in Table 1. All information about geographical locality, kind of material, dates, number of eggs, presence or absence of medicinal plants, fungi, and infertile eggs are listed together

An association of *A. lumbricoides* and *T. trichiura* occurs in nearly 59% of the archaeological findings all over the world. In Europe, it reaches more than 78%, and nearly 90% during the Middle Ages

We found a paradox in that for the prehistoric South America, *T. trichiura* is more common than *A. lumbricoides* and often is unassociated with *A. lumbricoides*. The findings of *T. trichiura* were more frequent, and even more impressive, when they were considered alone. *T. trichiura* eggs were found without *A. lumbricoides* eggs two times as often as *A. lumbricoides* without *T. trichiura*. The systematic search clearly defined the *Ascaris-Trichuris* paradox as a prehistoric American phenomenon. This phenomenon is also observed in the oldest European archaeological sites, but changed after Neolithic period (Bouchet et al., 2003; Gonçalves et al., 2003). However, the paradox emerged clearly in South America where results are almost completely limited to *T. trichiura* alone. There are 16 references for *T. trichiura* and only five for *A. lumbricoides*, and

two of these occurred in Spanish skeletons dated to colonial times

As for North America, there are two more finds of *A. lumbricoides* without *T. trichiura*. Indeed, for North America, there is only one prehistoric association of *A. lumbricoides* with *T. trichiura*. The majority of prehistoric North American sites have neither *A. lumbricoides* nor *T. trichiura* (Reinhard, 1990, 1992). Africa and Oceania are underrepresented regarding paleoparasitological finds, and so any inference is not reliable (Table 1)

The findings of *T. trichiura* eggs alone are also impressive in Europe and Asia. There are 12 references for *T. trichiura* and four for *A. lumbricoides*; this difference is bigger in Asia, where there are five *T. trichiura* egg finds alone, and only one for *A. lumbricoides*

3. Discussion

As observed in Table 1, the findings of *T. trichiura* eggs are more abundant than *A. lumbricoides* in South American archaeological material. Leles et al. (2008) by molecular diagnosis tested samples from archaeological sites South American, which were positive for *T. trichiura* eggs but negative for *A. lumbricoides* eggs by optical microscopy. These samples that were *A. lumbricoides*-negative by optical microscopy revealed DNA of *A. lumbricoides* through molecular analysis. These results point to a subdiagnosis of *A. lumbricoides* infection. Subdiagnosis means the identification of cryptic infections through alternative methods to microscopy

This finding is noteworthy and begs the question, why were *A. lumbricoides* eggs not found by microscopy in these samples? Three factors discussed below may be at play in the general lack of *A. lumbricoides* eggs in prehistoric material

3.1. Differences in disease factors –mediaeval Europe and prehistoric Americas

A. lumbricoides and *T. trichiura* are fecal-borne parasites. As such, there are behavioral factors that contribute to the control or proliferation of infection (Reinhard, 1988, 1990, 1992). Infection proliferates in sedentary, crowded communities with poor sanitation, inadequate hygiene, egg-contaminated food and water sources, with no access to medicines. In contrast, infection is controlled in communities that lack these characteristics as detailed by pathoecologists (Martinson et al., 2003; Reinhard, 2008; Reinhard and Bryant, 2008; Santoro et al., 2003). Seasonal or nomadic communities of small numbers of people have the best protection from infection because they come into contact with fecal-contamination rarely. Sedentary communities that have low populations which disperse over large areas for agriculture and hunting have only a slightly larger risk of infection. Sedentary communities of large populations which reside more-or-less permanently in close quarters around contaminated water have the greatest risk of fecal-borne infection. In crowded cities with poor sanitation, high levels of poverty, and poor sources of uncontaminated food and water, exposure to fecal-borne infections is inevitable

The latter conditions typified historic cities in Europe and North America (Jones, 1982, 1984; Reinhard, 1990; Fisher et al., 2007). In urban archaeological sites, *A. lumbricoides* and *T. trichiura* can be found in virtually any context including latrines, yards, and streets. However, the hunter-gatherer and horticulture sites of the prehistoric Americas have widely varying living conditions in which fecal-contamination was low relative to historic European and America cities. As detailed by pathoecological study (Reinhard, 1988, 2007, 2008; Reinhard and Bryant, 2008), in the prehistoric communities of the Americas, relatively small alterations in behavior could virtually eliminate infection by fecal-borne parasites. It is from this perspective that we present the following discussions

Table 1. Find of *Ascaris* (A) and/or *Trichuris* (T), locality, country and date

Site/Locality	Area	Date	Material	Parasite		References
				A	T	
<i>Europe</i>						
Grande Grotte, Arcy-sur-Cure, Yonne	France	30.160 ± 140– 24.660 ± 330 BP	Sediment and coprolite	+	–	Bouchet et al. 1996.
Shillouro-kambos	Cyprus	8300–7000 BC	Sediment from burial	+	+ ^d	Harter et al. 2005
Khirokitia, Larnaka	Cyprus	8300–7000 BC	Sediment from burial	+	+	Harter et al. 2005
Gwent levels at Goldcliff, northern side of the Severn estuary	Wales	5740–5620 BC cal	Sediment	–	+ ^a	Dark, 2004.
Clairvaux, Jura	France	3100–2700 BC	Sediments	+	+ ^j	Dommelier-Espejo, 2001
Swifterbant	Holland	5400 ± 40–5230 ± 40 BP	Coprolites	–	+ ^a	Roever-Bonnet et al. 1979
Arbon, Thurgau	Swiss	3384–3370 BC	Coprolites and sediments	+	+ ^j	Dommelier-Espejo, 2001
Ötzal	Austria	5300–5200 BP	Samples from the colon of the mummy	–	+	Aspöck et al. 1996.
Chalain, Jura	France	3200–3150 BC	Coprolites	–	+	Dommelier et al. 1998
Chalain, Jura	France	3044–2980 BC	Coprolites	–	+	Dommelier et al. 1998
Chalain, Jura	France	3080–2950 BC	Sediments and coprolites	–	+ ^c	Bouchet et al. 1995
Chalain, Jura	France	3200–2500 BC	Sediments and coprolites	–	+	Dommelier-Espejo, 2001
Brean Down, Somersset	England	Bronze Age	Sediment	+	+	Jones et al. 1988
Hulin, Central Moravia	Czech Republic	1600–1500 BC	Skeleton	+	+	Šebela et al., 1990
Drobintz girl	Prussia	600 BC	Contents of the bowel	+	+	Szidat, 1944
Hallstatt	Austria	2300 years	Excrements	+	+ ^{jd}	Aspöck et al. 1973
Tollund and Grauballe Man, Central Jutland	Denmark	3rd–5th century AD	Material from stomach	–	+	Helbaek, 1958.
Vilshofen	Germany	150–140 BC	Latrine	–	+	Specht, 1963
Hallein, Salzburg	Austria	2000 years	Excrements	–	+	Aspöck et al. 1973
Bremerhaven	Germany	100 BC–500 AD	“Terp” refuge mound	+	+	Jansen and Over, 1962
Valkenburg on Rhine	Holland	42–100 AD	Sediment	+	+ ^d	Jansen and Over, 1966
Lindow Man	England	Iron Age	Small intestine	+ ^e	+ ^j	Jones, 1986
Bobigny	France	2nd century AD	Burial	+	+	Rousset et al. 1996
York	France	2nd–3rd century AD	Sewer System	+ ^a	+	Wilson and Rackham, 1976
Place d’Armes, Namur	Belgium	II–III century AD	Material of cesspit	+ ^{af}	+ ^a	Rocha et al. 2006
Karwinden Man	Prussia	500 AD	Contents of the bowel	+	+	Szidat, 1944
Ribe	Denmark	750–800 AD	coprolite	+	+	Nansen and Jørgensen, 1977
York	England	9th–12th century AD	Soil, latrine, cesspits and coprolites	+	+ ^j	Jones, 1984
Coppergate, York	England	10th–11th century AD	Material of pits	+	+ ^{jb}	Hall et al. 1983
Winchester	England	1000 years	Pit soil	+ ^a	+ ^{ja}	Pike, 1967 and Pike, 1968
St. Isidoro’s Collegiate-Basilica, Leon	Spanish	X–XIII century AD	Mummy abdominal cavity	+ ^{if}	+	Hidalgo-Argüello et al., 2003
Place d’Armes, Namur	Belgium	IX–XI (1055 AD)	Pit	+ ^a	+ ^a	Rocha et al. 2006
Place d’Armes, Namur	Belgium	1055–1100 AD	Latrine	+ ^a	+ ^a	Rocha et al. 2006
Place d’Armes, Namur	Belgium	XII–XIII centuries	Latrine	+	+	Rocha et al. 2006
Place d’Armes, Namur	Belgium	XIV–XV centuries	Latrine	+	+	Rocha et al. 2006
Place d’Armes, Namur	Belgium	XV–XII (1618 AD)	Latrine	+	+	Rocha et al. 2006
Place d’Armes, Namur	Belgium	1611–1828 AD	Latrine	+ ^a	+ ^a	Rocha et al. 2006
Winchester	England	11th–12th century	Pit	+ ^a	+ ^{ja}	Taylor, 1955
Paris	France	XII–XV	Coprolites, sediments and latrines	+	+	Bouchet et al. 1989
Rue de Lutèce, Paris	France	XIV–XV	Sediments and coprolites	+	+	Bouchet, 1993
Southampton	England	13th–14th century AD	Contentes of cesspit soil	+ ^a	+ ^{ja}	Pike, 1975
Stroosteeg, Utrecht	Holland	13th–14th AD	Material from cesspits	+	+	Boersema and Jansen, 1975
Southwark	Europe	Middle ages	Soil	+	+	Rouffignac, 1987
Bermondsey, Abbey, Southwark	Europe	Middle ages	Soil	+ ^{ac}	–	Beard, 1986
Beauvais	France	XIII–XVII	Sediments, pits and garbage dumps	+	+	Bouchet, 1991
The Cour Napoleon, Paris	France	XI–XVI	Sediments of pit	+ ^{ac}	–	Bouchet, 1995
The Cour Napoleon, Paris	France	XI–XVI	Sample under skeleton of piglets	–	+ ^a	Bouchet, 1995
The Carrousel, Paris	France	XI–XVI	Excrements	+	+	Bouchet, 1995
Worcester	England	15th century	Barrel-latrine	+ ^{ab}	+ ^{abdj}	Greig, 1981 and Moore, 1981
Union Terrace, York	England	14th–16th century AD	Sediments from Stone-built latrine	–	+	Jones et al. 1988
Union Terrace, York	England	14th–16th century AD	Sediments from Stone-built latrine	+	–	Jones et al. 1988
Oslo	Norway	15th century AD	Cess-pit	+	+	Jones, 1982
Schleswig	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Berlin	Germany	Middle ages	Latrine soil	+	+ ^{jd}	Herrmann, 1985
Breisach	Germany	Middle ages	Latrine soil	+ ^j	+	Herrmann, 1985
Lübeck	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985 and Herrmann and Schulz, 1986

Table 1. Find of *Ascaris* (A) and/or *Trichuris* (T), locality, country and date (continued)

Site/Locality	Area	Date	Material	Parasite		References
				A	T	
Braunschweig	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Halmeln	Germany	Middle ages	Latrine soil	+	+ ^{jd}	Herrmann, 1985
Höxter	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Landshut	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Freiburg	Germany	15th century Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985 and Reinhard et al., 1988
Göttingen	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Marburg	Germany	Middle ages	Latrine soil	+ ⁱ	+	Herrmann, 1985
Regensburg	Germany	Middle ages	Latrine soil	+	+ ^j	Herrmann, 1985
Oldenburg	Germany	Middle ages	Latrine soil	+	+	Herrmann, 1985
Vincennes	France	800 AD	Sediments	+	+	Bouchet et al. 2003
Londres	England	XV–XVI	Sediments and latrines	+	+	Greig, 1982
Strasbourg	France	XV–XVI	Latrines	+	+	Legendre et al. 1986
Montbeliard, Doubs	France	XV	Material from cesspit deposits	+	+	Bouchet and Paicheler, 1995
Montbeliard, Doubs	France	15th–16th century AD	Sediments	+	+	Gonçalves et al. 2003
Raversijde	Belgium	16th century AD	Sediments from latrine	+	+	Fernandes et al. 2005
Paris	France	XVII–XVIII	Sediments	+	+	Bouchet et al. 1991
Marly-le-Roy, Yveline	France	17th–18th century AD	Latrine	+	+	Bouchet et al. 1998
Namur	Belgium	18th century AD	Sediments	+	+	Gonçalves et al. 2003
Subtotal of findings				62	70	
Subtotal of isolate findings				4	12	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				58		
<i>Africa</i>						
Kruger Cave, Rustenburg	South Africa	10000–7000 BP	Coprolite	+ ^{ab}	+ ^{abj}	Evans et al. 1996
Nile valley	Nubia	2400 BC–1500 AD	Visceral in canopic jars	–	+	Bouchet et al., 2003 and Harter and Bouchet, 2006
PUMII mummy	Egypt	200 BC	Intestinal tissues of a mummy	+	–	Cockburn et al. 1975
Akhthep's mastaba of Saqqara	Egypt	715–656 BC	Embalming waste jar	+	–	Harter et al. 2003
K2, Greefswald	South Africa	1000–1300 AD	Coprolite	–	+	Dittmar and Steyn, 2004
Subtotal of findings				3	3	
Subtotal de of isolate findings				2	2	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				1		
<i>Asia</i>						
Jerusalem	Israel	7th–6th century BC	Remains of bathroom	–	+	Unpublished observations
Jiangling County, Hubei Province	China	2300 years ago; Chu Dynasty, the Warring Stage (475–221 BC)	Ancient corpse from tomb, Chu Dynasty mummy	–	+	Yang et al., 1984 and Su, 1987
Hubei Province	China	167 BC	Han Dynasty mummy	–	+	Liangbiao and Tao, 1981 and Cheng, 1984
Ma-Wang-Dui, Changsha city, Hunan Province	China	2100 years ago (206 BC–220 AD during Han Dynasty)	Rectum and liver of mummy	–	+	Wei, 1973.
Nahal-Mishmar Valley	Israel	160 AD	No available	–	+	Witenberg, 1961
Acre	Israel	1300 AD	Latrine	+	–	Mitchell and Stern, 2000
Schinchang-dong, Kwangju city	Korea	100 BC	Soil (plant layer major) probably in the house where human bones were found	+	+	KNM, 1997.
Chilgok-gun, Taegu, Gyeongsangbuk Province	Korea	668–935 AD (Unified Shilla Dynasty)	Pit soil in some place where toilet may be exist	+ ^{afj}	+ ^a	Han et al. 2003.
Fujiwara Palace Site	Japan	710 AD	Sediment of the pit	+	+ ^j	Matsui et al. 2003
Yangju	Korea	1411 ± 42 AD (Chosun Dynasty)	Rectal tissue of the mummy	+ ^e	+ ^j	Seo et al. 2007
Joseon Dynasty	Korea	Late 17th Century	Mummy	+	+	Shin et al. 2008
Subtotal of findings				6	10	
Subtotal of isolate findings				1	5	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				5		
<i>Oceania</i>						
Wellington	New Zealand	150–200 years ago	Coprolite	+	–	Andrews, 1976
Subtotal				1	0	
Subtotal of isolate findings				1	0	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				0		

Table 1. Find of *Ascaris* (A) and/or *Trichuris* (T), locality, country and date (continued)

Site/Locality	Area	Date	Material	Parasite		References
				A	T	
<i>North America</i>						
British Columbia	Canada	3700–3490 cal BC	Midden sediments	+	–	Bathurst, 2005
Upper Salts Cave, Kentucky	USA	570–290 BC	Coprolite	+	–	Fry, 1974
Big Bone Cave, Tennessee	USA	2177–145 BP	Coprolite	+	–	Faulkner et al. 1989
Antelope House, Arizona	USA	900–1250 AD	Coprolite and Latrine	+	–	Gonçalves et al. 2003
Elden Pueblo, Arizona	USA	1070–1250 AD	Latrine soil	+ ⁹	+ ^{9j}	Hevly et al., 1979 and Reinhard et al., 1987
Adak Island, Alaska	USA	840 ± 40 BP	Samples from abdominal cavity	+	–	Bouchet et al. 2001
Albany, New York	USA	1600–1700 AD		+ ^{fi}	+	Fisher et al. 2007
Newfoundland	Canada	17th century AD	Privy contents	+ ^a	+ ^a	Horne and Tuck, 1996
Colonial Williamsburg, Virginia	USA	1720 AD	Fecal layer latrine	+	+ ^j	Reinhard, 1990
New Brunswick, New Jersey	USA	1790–1899 AD	Sediments from latrines	+ ^{fi}	+	Unpublished observations
Queen Ann Square, Newport, Rhode Island	USA	18th century AD	Privy soils	+	+ ^j	Reinhard et al. 1986.
Lutheran Church, Pearl Street, Albany, New York	USA	1790s	Sediments from privy or trash pit	+	+ ^j	Reinhard, 2004.
Wilmington, Delaware	USA	19th century AD	Privy contexts	–	+	Fries et al. 1990
Greenwich Village, New York City, New York	USA	19th century AD	Latrine soil	–	+	Reinhard, 1990.
Fayette, Michigan	USA	19th century AD	Sediments from privies	–	+	Faulkner et al. 2000
Manhattan, Kansas	USA	1860–1900	Sediments of skeletons	+ ^j	+	Le Bailly et al. 2006
Wong Nim's Property, San Bernardino, California	USA ^h	1880–1930 AD	Sediments from latrine	+	+	Reinhard et al. 2008
Philadelphia	USA	Historic period	Sediments	+	+ ^{di}	Unpublished observations
Subtotal				15	13	
Subtotal of isolate findings				5	3	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				10		
<i>South America</i>						
Lapa Pequena, Minas Gerais	Brazil	8000–7000 BP	Coprolite	–	+	Gonçalves et al. 2003
Huarmey Valley	Peru	4277 ± 181 BP	Coprolite	+ ^e	–	Patrucco et al. 1983
Boqueirão Soberbo, Minas Gerais	Brazil	4905 ± 85–1325 ± 60 BP	Coprolite	–	+	Ferreira et al. 1982
Santa Elina, Mato Grosso	Brazil	4000–2000 BP	Coprolite	–	+	Gonçalves et al. 2003
Orejas de Burro 1	Argentina	3720–3978 BP cal	Sediment from abdominal cavity of skeleton	–	+	Fugassa and Barberena, 2006
Gentio II Cave, Minas Gerais	Brazil	3490 ± 120–430 ± 70 BP	Coprolite and mummy intestinal contents	+	+	Ferreira et al., 1980, Ferreira et al., 1983 and Gonçalves et al., 2003
Tulán, San Pedro de Atacama	Chile	1080–950 BC	Coprolite	–	+	Gonçalves et al. 2003
Estrago Cave, Pernambuco	Brazil	2000 BP	Coprolite	–	+	Ferreira et al. 1989
Huarmey Valley	Peru	1000 AD	Coprolite	–	+	Patrucco et al. 1983
San Gerónimo	Peru	1020–1156 AD	Coprolite	–	+	Martinson et al. 2003
Lluta Valley	Chile	Inca Late and Intermediate Period	Coprolite	–	+	Santoro et al. 2003
Vale Alto de Ica	Peru	725 AD (Late Nasca)	Coprolite	+	–	Gárate et al. 2005
Cerro El Plomo, Santiago	Chile	450 years	Feces from rectum	–	+	Pizzi and Schenone, 1954
El Potrero de Santa Lucía, Andalgala, Catamarca	Argentina	470 ± 200 BC 650 ± 80 AD 310 ± 90 AD	Sediments	–	+	Pau et al. 2005
Nombre de Jesús	Argentina ⁱ	XVI	Sediments	+ ⁹	+ ^{9j}	Fugassa and Guichón, 2006 and Fugassa et al., 2006
Nombre de Jesús	Argentina ⁱ	XVI	Sediments	+	–	Fugassa et al. 2007
Mummy pre-Columbian, Murga culture	Peru	Colonial period	Colon contents of a mummy	–	+	Fouant et al. 1982
Itacambira, Minas Gerais	Brazil	18th century AD	Colon contents of a mummy	–	+	Araújo et al. 1984
Pedra Furada	Brazil	Not available	Coprolites	–	+	Gonçalves et al. 2003
Subtotal				5	16	
Subtotal of isolate findings				3	14	
Subtotal of <i>Ascaris</i> and <i>Trichuris</i> association				2		

Table 1. Find of *Ascaris* (A) and/or *Trichuris* (T), locality, country and date (continued)

Site/Locality	Area	Date	Material	Parasite		References
				A	T	
Total				92	112	
Total of isolate findings				16	36	
Total of <i>Ascaris</i> and <i>Trichuris</i> association					76	

BP Before Present, BC Before Christ, AD Anno Domini

- a. Uncertain human origin
- b. Presence of vermifuges plants or plant parasitic nematode
- c. Uncertain diagnosis
- d. Samples positive for *Trichuris* and negative for *Ascaris*
- e. Unfertilized eggs
- f. Samples positive for *Ascaris* and negative for *Trichuris*
- g. Presence of fungi
- h. Origin of the infection is probably from Asia
- i. Infection is probably from Europe
- j. Eggs most abundant of the two species

3.2. Medicinal plant use and reduced infection level

In communities that are not constantly challenged by fecal-borne parasites, even the occasional use of anthelmintics reduces or eliminates infection. There is no doubt that prehistoric peoples in the Americas had an extensive pharmacopeia based on native medicinal plants (Chaves and Reinhard, 2006; Moerman, 2009; Reinhard et al., 1985). Palynological analyses reveals that three plant genera were used to treat parasite infection or symptoms of parasite infection in northeastern Brazil some 7000 years ago (Chaves and Reinhard, 2006). Seed analysis of coprolites dating to nearly 9000 years ago from the Colorado Plateau suggest that anthelmintic plants were a part of ancient diet (Reinhard et al., 1985). An Aztec codex illustrates the use of anthelmintic species up to the Spanish Entrada (de Montellano, 1975). These examples illustrate the long-standing and widespread availability of medicines throughout prehistory

Anthelmintics, whether natural or synthetic, are more effective for *A. lumbricoides* than *T. trichiura* (Muchiri et al., 2001; Reinhard, 2004; Saathoff et al., 2004; Zani et al., 2004). Keiser and Utzinger (2008) performed a systematic review and a meta-analysis to evaluate four medicines used for intestinal helminths. Single doses are effective for *A. lumbricoides*, but unable to eliminate *T. trichiura*. This has been borne out in the archaeoparasitology of North American historic sites and especially Albany, New York (Fisher et al., 2007). The latrines of higher class individuals with access to vermifuges show a reduction of *A. lumbricoides* eggs relative to poor households. However, the numbers of *T. trichiura* eggs is comparable for all economic classes

The differential effects of vermifuges on these worms has been documented in recent indigenous villages. Communities in the Amazon such as Santa Isabel do Rio Negro, are descendants of indigenous societies that were demographically concentrated, assimilated and acculturated in historic times. The Santa Isabel do Rio Negro community is monitored for prevalence of helminths and frequently treated with drugs as medicated mebendazole and/or self-medicated with natural plants. It has been observed over the years that the prevalence of *A. lumbricoides* decreased and *T. trichiura* increased (Bóia et al., 2006; Carvalho-Costa et al., 2007). These observations agree with the review done by Keiser and Utzinger (2008). In other words, the effect of anthelmintics on modern villages models prehistoric parasite control

Whipworms are adapted to the large intestine. They attach to the intestine by burrowing their anterior extremity into host

mucosa. *A. lumbricoides*, however, lives freely in the gut lumen. *A. lumbricoides* worms maintain their place in the lumen by muscular exertions against the flow of the intestinal contents under peristalsis. Thus, roundworms are not attached to the lumen and are more susceptible to the effects of anthelmintic compounds

When we compare the possibility of *T. trichiura* and *A. lumbricoides* being eliminated from the host, roundworms will be less resistant to all treatments, be it mechanical such as high fiber content or drugs such as medicinal plants ingested by the host. In coprolites from North America, great amounts of insoluble fiber are commonly found. This high fiber could contribute to the elimination of *A. lumbricoides* adult worms

Chenopodium is a genus with some species that have vermifugic action. Vermifugic chenopods were mentioned in five articles, and point to a possible explanation to negative results of *A. lumbricoides* eggs (Dommelier et al., 1998; Greig, 1981; Hall et al., 1983; Reinhard et al., 1987; Reinhard, 1990). *Chenopodium* sp. and *Bauhinia* sp., another plant with anthelmintic properties were found in some South American coprolites (Chaves and Renault-Miskovsky, 1996; Chaves and Reinhard, 2006)

The abundant ethnographic and archaeological evidence of prehistoric anthelmintics in the New World, and the differential

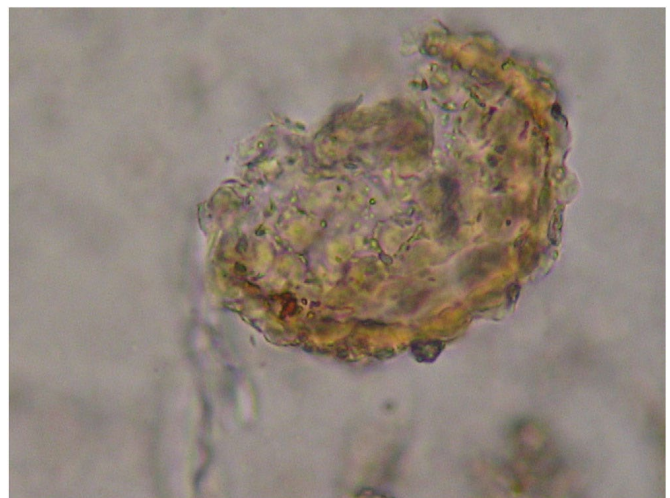


Figure 1. A poorly preserved *A. lumbricoides* egg represented only by a partial mammillated outer shell.

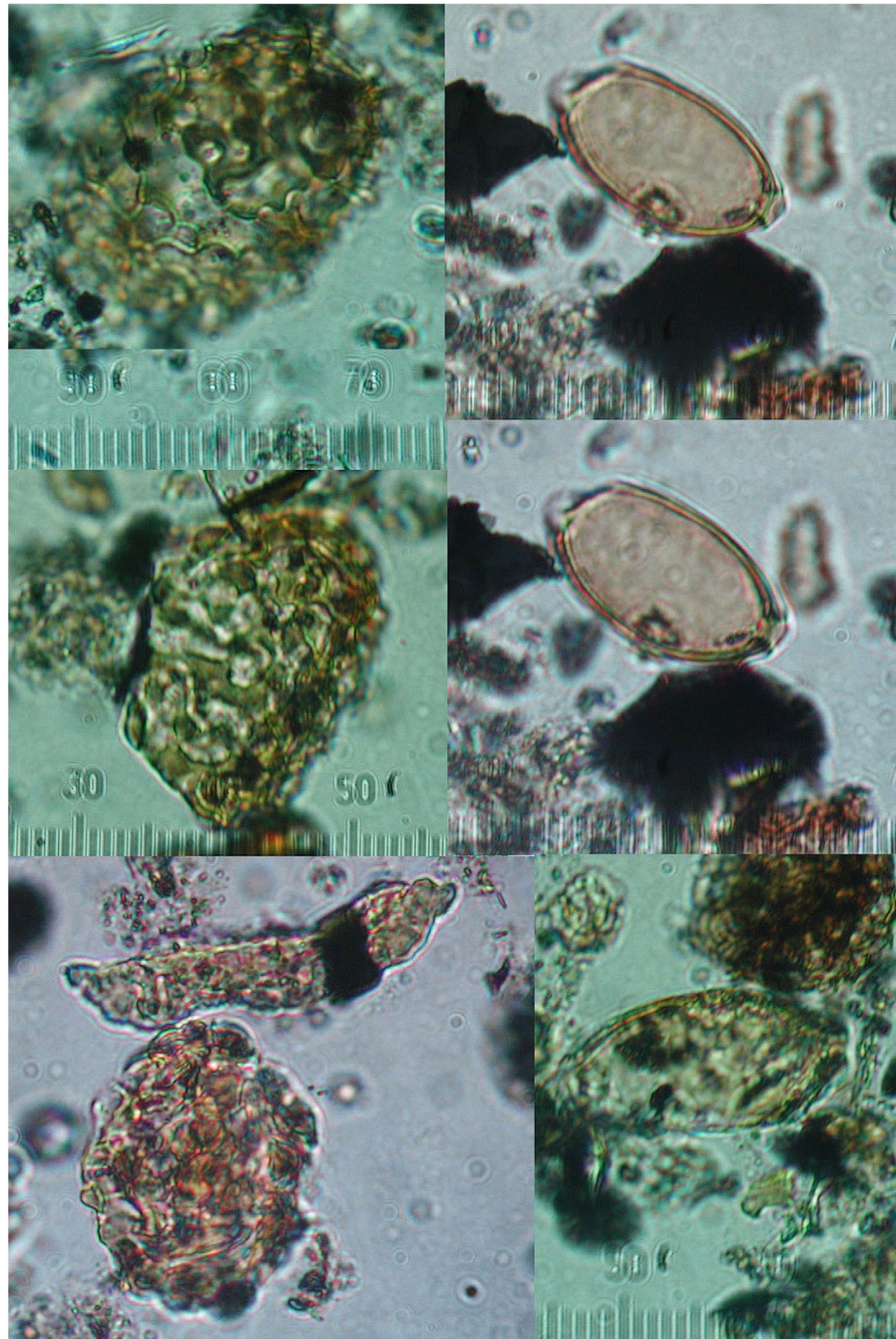


Figure 2. The series of images on the left shows moderate to poor preservation of *A. lumbricoides* eggs. The upper images shows partial erosion of the mammillated coat. The center image shows a deformed egg and the lower image shows a shrunken egg. The right series shows moderate preservation of *T. trichiura* eggs. The upper images focus on two plane of the same egg and show details of one operculum that is still in place. The other side of the egg is fractured. The lower image shows an egg partially encrusted with sediment and a partially fractured wall.

resistance of *T. trichiura* and *A. lumbricoides* to the effects of anthelmintics, is very important to the enigmatic absence of *A. lumbricoides*. As reviewed by Reinhard et al. (1985), the Aztecs, among others, had effective anthelmintic and prophylactic remedies derived from native plants. The absence of eggs may well be due to the difficulty of reaching patency in human populations that habitually used anthelmintics. In addition, it appears from the work of Andrew Jones that infection with *A. lumbricoides* and *T. trichiura* was an unavoidable aspect of European urban life from Medieval times onward. This was not the case in the New World where poor sanitation was not as

significant a problem. Therefore, basic anthelmintics were sufficient to keep *A. lumbricoides* at minimal infection levels

3.3. Environment and taphonomy

It might be possible that differential preservation of the eggs of *A. lumbricoides* and *T. trichiura* results in the post-depositional decay of one type of egg over the other. Thus, taphonomy must be discussed as a potential contributor to the paradox

The eggs of *A. lumbricoides* have two durable layers, each resistant to different conditions. The inner layer is a chitin shell. The outer layer is a thick, mammillated, albuminoid protein

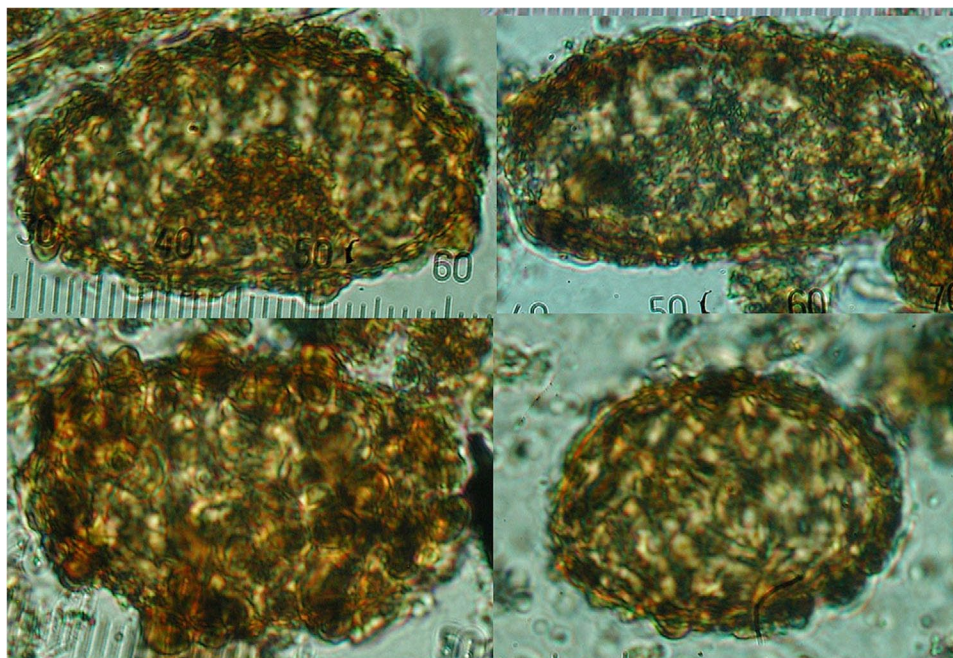


Figure 3. These *A. lumbricoides* eggs from a historic site in Albany, New York show one fertilized egg (lower right) and three unfertilized eggs. Relative to the smaller, oval fertilized egg, unfertilized eggs are larger, more block-shaped, with a coarser mammillated coat

coat. When the chitin shell is destroyed, the out albumin coat can still be recognized. More commonly, the albumin coat deteriorates and the chitin egg persists. These are called decorticated eggs and are also easily recognizable

T. trichiura eggs are among the most recognizable in parasitology. The lemon or barrel shaped eggs taper at the poles to operculated apertures with inwardly beveled edges. The distinctive shape of these eggs makes them recognizable even when badly corroded from archaeological contexts

Because of the layered structure of *A. lumbricoides* eggs, one might think that they are more durable than *T. trichiura* eggs. This is not always the case. Kobayashi et al. (1984) experimentally contaminated soil with *A. suum* eggs submitted to different temperature conditions. They recovered the eggs and evaluated degeneration and embryonation after different times. It was observed that on surface almost 100% of the eggs degenerated and consequently did not embryonate. Larsen and Røpstorff (1999) contaminated short grass study plots, 2 cm below the surface of well-cultivated bare soil with *A. suum* and *T. suis* eggs, and evaluated the recovery of eggs submitted to different temperature conditions. Results showed that the disappearance of *A. suum* eggs was significantly greater than that of *T. suis*. This difference is greater yet during sunny months. This points to different eggshell vulnerabilities in the two genera. Therefore, this probably occurred in the past with open environments. If so, the increased destruction of *A. lumbricoides* would have resulted in fewer infections. Also, in some contexts, the exclusive recovery of *T. trichiura* eggs may reflect environmental factors resulting in differential preservation

Well-preserved eggs of *A. lumbricoides* and *T. trichiura* have been reported in archaeological sites in the majority of published articles. Szidat (1944) and Taylor (1955) described the extraordinary preservation of *T. trichiura* eggs. However, Andrews (1976) and Jones (1986) report finding identifiable fragments of *A. lumbricoides* broken eggshell. Bathurst (2005) also reports many broken *A. lumbricoides* eggs, and Fugassa et al. (2006) found fragments of *A. lumbricoides* eggs in Patagonian sediments. Pike (1967) and Seo et al. (2007) observed eggs

decorticated and uncoated. In different materials examined in our laboratories we also observed broken *A. lumbricoides* eggs (Figure 1). This suggests that preservation potential varies between archaeological contexts (Figure 2)

3.4. Nematophagous fungi

Biological control has been promoted as a way to reduce intestinal helminth prevalences, especially animal parasites that show increased resistance to anthelmintics (Larsen, 1999). Nematophagous fungi are natural predators of nematodes. Currently, 150 species are known, divided in three groups: nematode predators, endoparasites, and egg opportunistic parasites (Gray, 1987). Many genera, such as *Arthrobotrys*, *Duddingtonia*, *Pochonia* and *Monascroporium* are efficient in controlling animal intestinal parasitosis (Wang et al., 2008; Araújo et al., 2009a, 2009b; Braga et al., 2009a, 2009b; Carvalho et al., 2009; Kelly et al., 2009; Maciel et al., 2009a, 2009b). These fungal taxa are distributed throughout the world and in every kind of climate (Gray, 1987). Braga et al. (2007) proved that *Verticillium chlamydosporium* kills eggs of *A. lumbricoides*. Araújo et al. (2008) showed that *Pochonia chlamydosporia* attacked *A. suum* eggs. Some nematophagous fungi have been found in regions near archaeological sites in Minas Gerais state, central Brazil (Ribeiro et al., 1999, 2003)

However, few paleoparasitological analyses mentioned the presence of nematophagous fungi. Fugassa et al. (2006) mention the presence of fungal spores and hyphae in the sediment recovered from the pelvic girdle of a skeleton dated of the 16th century. Reinhard et al. (1988) describe fungal attack on both ascarid and trichurid eggs in latrine sediments

However, preferential fungal attack may explain the low number of eggs found in some archaeological sites, but it would not explain the absence of one parasite when the other one is present, i.e., it would not explain the absence of *A. lumbricoides* eggs and the presence of *T. trichiura*, unless different biological aspects regarding *A. lumbricoides* and *T. trichiura* shell egg resistance are involved to allow destruction of one parasite eggs instead of the other. These preliminary observations indicated

that examination of fungal attack on parasite eggs would be a fruitful and important line of research that should be developed

4. Conclusions

Prehistoric inhabitants of the Americas had behavioral factors that limited exposure to fecal-borne parasites. Contributing to the rarity of *A. lumbricoides* infection, use of medicinal plants differentially expelled ascarids more than whipworms. Taphonomic factors differentially destroyed the infective eggs of ascarids more than whipworms. Finally fungal attack may have destroyed the infective stages of ascarids and their evidence in archaeological contexts. Thus, the reduction of ascarids in prehistoric sites reflects several aspects of prehistoric ecology that limited infection

The main conclusion of this review is that paleoparasitological analysis should involve multidisciplinary teams, with experts in medicinal plants, nematophagous fungi, and taphonomy. Statistical analysis must be performed whenever possible, be it to verify the morphology of eggs (Araújo, 1988; Confalonieri et al., 1988), or to evaluate differences in eggshell resistance/fragility when submitted to different environmental conditions. It is also important to quantify the number of eggs per volume and/or weight of sample. It is essential to specify whether *A. lumbricoides* eggs are fertilized or unfertilized (Figure 3). Unfertilized eggs signify precarious conditions for transmission and patent infection, or even cross infection between human and pig species (Peng et al., 2003)

However, *T. trichiura* eggs were observed in greater numbers even in environments where high temperatures did not prevail in the past. Therefore, unless *A. lumbricoides* decomposed 10 times more than *T. trichiura* (considering the recorded egg production for these species), a change in egg production over time cannot be discarded. Epidemiology and ecology studies showed that host-parasite relationships did not necessarily evolve to harmony over time. Sometimes virulence and pathogenicity increase, as expressed by high reproductive rates in micro and macroparasites (Galvani, 2003)

Most of the reported associations of *A. lumbricoides* and *T. trichiura* have been dated by radiocarbon method and geographically placed. Based on these data, it would be interesting to establish some relationships with climate and environmental conditions. Taphonomic processes might have been an important factor affecting paleodistribution of *A. lumbricoides* and *T. trichiura* reported up to now

Parasites, together with their hosts, change behavior patterns over time. One example was recently studied among the Surui, an Amazonian Indian group that was found negative for *A. lumbricoides* and *T. trichiura* infection, while the tapeworm *Hymenolepis nana* reached more than 20% prevalence. Interesting, the Surui prevalence rates were the inverse ten years ago (Palhano-Silva et al., 2009). Absence or low prevalence rates for *A. lumbricoides* and *T. trichiura* were also observed among Yanomami contemporary groups and prehistoric inferences were made reflecting ancient scenarios (Confalonieri et al., 1991). Thus, prehistoric sites with time depth should be studied for increase and/or decrease presence of eggs over time

Paleoparasitology is opening frontiers, and data are beginning to shed a light into evolutive strategies of these two important intestinal parasites over evolutionary time. What was before only theoretical suppositions can be now tested in paleoparasitological findings

Acknowledgments - We acknowledge Dr. Hun, for kindly answering our questions and verifying Asian finds; Dr. Mathieu Le Bailly for sending additional information from his articles.

This research was supported by Brazilian agencies CNPq, CAPES, PAPES/Fiocruz, FAPERJ

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